

NUTRIENT CONTENT OF FIVE SPECIES OF DOMESTIC ANIMALS COMMONLY FED TO CAPTIVE RAPTORS

NANCY J. CLUM¹

The Peregrine Fund, 566 W. Flying Hawk Lane, Boise, ID 83709 U.S.A.

MARIANNE P. FITZPATRICK AND ELLEN S. DIERENFELD

Department of Nutrition, Wildlife Conservation Society, 185th St. and Southern Blvd., Bronx, NY 10460 U.S.A.

ABSTRACT.—The objective of this work was to provide a basis for more informed evaluation of diet options with respect to the nutritional needs of captive raptors. We compared nutritional content of five domesticated species that are most commonly fed to captive raptors; quail (*Coturnix coturnix japonica*), chickens (*Gallus domesticus*), rats (*Rattus norvegicus*), mice (*Mus musculus*) and guinea pigs (*Cavia porcellus*). We measured proximate composition (moisture, lipid, protein, ash), vitamin A, vitamin E, copper, iron, zinc, magnesium, manganese, calcium and potassium. Significant species differences were found in lipid and in vitamins A and E, and differences approached significance in iron and manganese concentrations. Differences in nutrient content between species did not correspond to differences in nutrient levels of diets consumed by prey. All species contained adequate amounts of protein, lipid, vitamin A, calcium, magnesium and zinc. However, whole domesticated prey were potentially inadequate sources of vitamin E, copper, iron and manganese.

KEY WORDS: *body composition; minerals; nutrition; vitamins; raptor diet.*

Contentos de nutrimento para cinco especies de animales domesticos frecuentemente dados para comer ha rapaces captivos

RESUMEN.— El objetivo de este trabajo fue para proporcionar un base para una evaluación mas informada de opciones de dieta con respeto con la necesidad de alimentación de rapaces cautivas. Nosotros comparamos el contenido de nutrimento de cinco especie domesticadas que estén frecuentemente dadas de comer a rapaces cautivos: codorniz (*Coturnix coturnix japonica*), gallinas (*Gallus domesticus*), rata, (*Rattus norvegicus*), ratón (*Mus musculus*) y cobayo (*Cavia porcellus*). Nosotros medimos composición próximo (humedad, grasa, proteína, ceniza), vitamina A, vitamina E, cobre, fierro, zinc, magnesio, manganeso, calcio y potasio. Diferencia significas de especies fueron encontradas en grasa y en vitamina A y E y diferencias estaban significante en concentraciones de fierro y manganeso. Diferencias en alimento entre especie no correspondieron a diferente niveles de nutrimento de dietas consumidas para la presa. Todos contienen suficiente cantidad de proteína, grasa, vitamina A, calcio, magnesio y zinc. Sin embargo, presa domesticada fueron pontenciamente insuficiente de vitamina E, cobre, fierro y manganeso.

[Traducción de Raúl De La Garza, Jr.]

The diets of most wild raptors consist of a wide variety of prey species (Palmer 1988). Of necessity, raptors maintained in captivity are usually fed a very limited array of domesticated species. The diet of captive birds is therefore artificial in both the type and variety of species consumed. Few studies have been done regarding the nutritional status of free-ranging birds, but the data that do exist sug-

gest that wild birds may differ significantly from captive animals of the same species (Dierenfeld et al. 1989, Dierenfeld 1994). This is of concern to zoos, private breeders and conservation organizations that engage in captive propagation because nutritional status affects health (Gershwin et al. 1985, Sklan et al. 1995), growth (Lavigne et al. 1994a), reproduction (NRC 1984, Naber and Squires 1993) and longevity (Good and Gajjar 1986). Undernutrition can also have long-term effects (Bedi 1987, Grantham-McGregor 1987, Lavigne et al. 1994b), and can, therefore, potentially influence the viability of reintroduced populations.

¹ Present address: Environmental Science Program, DePaul University, 1036 West Belden Ave., Chicago, IL 60614.

For most individuals and organizations, no feasible alternative exists to feeding artificial diets. For financial and logistical reasons, options are usually restricted to prepared commercial diets or to one or more domesticated species. Relatively little information is available on the nutrient content of whole vertebrate prey (see Dierenfeld et al. 1994 for review) to facilitate comparison of dietary options. Furthermore, existing nutritional information focuses primarily on macronutrients such as lipid, protein, ash and fiber which are less likely to be limiting in the diet of captive animals than vitamins or minerals.

This study compares nutritional content of five domesticated species that are among the most commonly fed to captive raptors: quail (*Coturnix coturnix japonica*), chickens (*Gallus domesticus*), rats (*Rattus norvegicus*), mice (*Mus musculus*) and guinea pigs (*Cavia porcellus*). We measured proximate composition (moisture, lipid, protein, ash), vitamin A, vitamin E, copper (Cu), iron (Fe), zinc (Zn), magnesium (Mg), manganese (Mn), calcium (Ca) and potassium (K). These results provide the basis for a more informed evaluation of diet options with respect to the nutritional needs of captive raptors.

METHODS

Experimental Design. We analyzed five species of domesticated animals. Both male and female quail were analyzed, but only males of other species were used because females are typically retained for breeding stock at our facility. Birds ($N = 50$, each species) were raised from hatch to 6 wk of age in brooders. Mammals were raised in litters until weaning. Three individuals from each mammalian species (from different litters) were then randomly selected and placed together in new cages. Mice were raised to 12 wk, rats were raised to 11 wk and guinea pigs were raised to 10 wk in standard laboratory mammal cages. The following complete commercial products were fed, exclusively and *ad libitum*: quail, Purina Turkey Starter; chickens, Purina Meatbuilder; rats and mice, Purina Formulab Chow; guinea pigs, Purina Guinea Pig Chow (all manufactured by Purina Mills, St. Louis, MO U.S.A.).

Laboratory Analyses. Three individuals of each species (and each sex for quail) were ground separately. Feathers were removed from birds, as most raptors pluck their prey and the majority of feathers consumed are regurgitated in pellets; for this study we assume that nutrient intake from feather digestion is negligible. Guinea pigs were also decapitated as even the largest eagles held at our facility failed to consume the craniums of this species. Four samples were immediately taken from each individual; two for duplicate vitamin analyses and two for duplicate moisture, lipid, ash and mineral analyses. The remainder of the ground sample was frozen, and two

samples were taken at a later time for duplicate protein analyses. One sample was also taken from each type of feed fed to each species.

Moisture content was determined by drying samples to a constant weight in a vacuum oven at 60°C. Lipid content of dried samples was determined indirectly using Soxhlet extraction (Ellis 1984). Fat-free dry samples were ashed in a muffle furnace at 550°C for three days (Ellis 1984) to determine ash content. Protein content of thawed wet tissues was assayed by the Biuret method (Horwitz 1975); samples were corrected for any moisture loss during freezing by redrying a second set of samples. Tissue extraction and analyses of retinol and alpha- and gamma-tocopherol were modifications of the general methods of Taylor et al. (1976) as described in Douglas et al. (1994), using high performance liquid chromatography. Extraction of feed was performed according to the method described by Combs and Combs (1985). Vitamin A activity was calculated as 0.3 g all-trans retinol = 1 IU (Olson 1984). Vitamin E was calculated by summing alpha- and gamma-tocopherols, where 1 mg alpha-tocopherol = 1.1 IU and 1 mg gamma-tocopherol = 0.1 IU (Machlin 1984). Ashed samples were prepared for mineral analysis according to the method of Parker (1963). Ca, Cu, Fe, Zn, Mg and Mn levels were measured on a Perkin-Elmer atomic absorbance spectrometer.

Statistical Analyses. Species differences in nutrient content were analyzed using a one-way ANOVA in SYSTAT (Wilkinson 1990). Sex differences and comparisons between pairs of species were analyzed using the Mann-Whitney *U*-statistic or the Student's *t*-test. Comparisons among more than two species were analyzed with a Kruskal-Wallis test. Where the same test was performed on multiple dependent variables, critical *P*-values were corrected for multiple comparisons using a sequential Bonferroni method (Rice 1989). Significance was assigned at the level of (corrected) $P \leq 0.05$.

RESULTS

Female quail were 17% heavier than male quail at 6 wk of age ($\text{mass}_{\text{males}} = 121.6 \text{ g}$, $\text{SE} = 12.6$, $\text{mass}_{\text{females}} = 146.5 \text{ g}$, $\text{SE} = 8.9$, $t = 5.91$, $P = 0.00001$). No sex differences were found in proximate composition, vitamin A and vitamin E content, or mineral levels (Table 1), although females had consistently higher levels of all vitamins and minerals (Sign test, $z_c = 2.5$, $P = 0.008$). Values for male and female quail were therefore combined in subsequent analyses.

Significant species differences were found in lipid (Table 2), vitamin A and vitamin E (Table 3) and differences approaching significance (adjusted $P < 0.06$) in Fe and Mn concentrations (Table 3). Lipid levels were lowest in mice and highest in guinea pigs and chickens. Mice were 10 times higher in vitamin A than rats (Mann-Whitney, $U = 18.0$, $P = 0.02$), the species containing the next highest vitamin A values. Rats, quail and chickens did not

Table 1. Mean nutritional content of whole male and female Japanese Quail.^a

	MALE	FEMALE	<i>P</i> ^b
Moisture (%)	65.1 (3.1)	65.6 (1.8)	0.827
Protein (%DM)	64.9 (14.6)	71.6 (6.8)	0.524
Lipid (%DM)	33.2 (6.3)	26.3 (3.2)	0.050
Ash (%DM)	9.6 (1.3)	12.0 (1.7)	0.127
Retinol (IU/kg)	32 989 (10 951)	66 444 (30 525)	0.127
Alpha-tocopherol (IU/kg)	41.6 (13.3)	79.3 (0.4)	0.050
Calcium (mg/kg)	32 685 (4178)	43 615 (6561)	0.127
Copper (mg/kg)	2.66 (0.61)	3.02 (0.77)	0.827
Iron (mg/kg)	85.07 (7.93)	112.40 (33.94)	0.275
Magnesium (mg/kg)	578.6 (255.2)	752.7 (209.3)	0.513
Manganese (mg/kg)	6.61 (2.11)	8.45 (4.31)	0.513
Zinc (mg/kg)	55.01 (9.13)	54.30 (26.66)	0.827

^a All data except moisture content presented on a dry matter basis. Values are means and one standard deviation. *N* = 3, each sex

^b Unadjusted *P*-values, Student's *t*-test. No comparisons significant following correction for multiple comparisons.

differ in vitamin A content (Kruskal-Wallis, $H = 0.641$, $P = 0.73$). Guinea pigs were 50% lower in vitamin A than chickens (Mann-Whitney, $U = 9.0$, $P = 0.05$), the species with the next lowest values. Guinea pigs also had vitamin E levels that were at least 50% lower than quail (Mann-Whitney, $U = 18.0$, $P = 0.02$); quail, mice and chickens were not significantly different in vitamin E content (Kruskal-Wallis, $H = 1.55$, $P = 0.46$). Rats were three times higher in vitamin E than mice (Mann-Whitney, $U = 9.0$, $P = 0.05$).

Chicken and quail were not significantly different in Fe content (Mann-Whitney, $U = 10.0$, $P = 0.80$) or Mn content (Mann-Whitney, $U = 15.0$, $P = 0.12$), but the avian species were significantly higher than the mammalian species in both Fe (Mann-Whitney, $U = 64$, $P = 0.04$) and Mn (Mann-Whitney, $U = 68$, $P = 0.02$). Within the mammals, mice contained more Fe than guinea pigs (Mann-Whitney, $U = 9.0$, $P = 0.05$) or rats (Mann-Whitney, $U = 9.0$, $P = 0.05$), but rats and guinea pigs did not differ from each other (Mann-Whitney, $U = 4.0$, $P = 0.827$). Guinea pigs and mice had sim-

ilar levels of Mn (Mann-Whitney, $U = 5.0$, $P = 0.275$) and were both higher in this nutrient than rats (Mann-Whitney, $U = 16.0$, $P = 0.05$). Differences in nutrient levels of feeds did not correspond to nutrient differences between species in any case (Table 4).

DISCUSSION

The differences between 6-wk male and female quail were not significant in this study; however, it is worth noting that females had consistently higher levels of most nutrients, as well as lower lipid levels, than males. We have also found that at 16 wk of age nutrient levels in male quail are unchanged relative to 6-wk old birds, but levels in female quail (mobilizing resources for egg production) have almost doubled (unpubl. data). These data suggest that sex differences in nutrient content may be detectable with larger samples sizes or at different ages.

With the exception of lipid content, little difference was observed in proximate composition among species. Our results are similar to published

Table 2. Proximate composition of whole domestic species.^a

	QUAIL	CHICKEN	RAT	MOUSE	GUINEA PIG	<i>P</i>
Moisture (%)	65.4 (2.3)	67.7 (1.3)	64.3 (2.4)	66.9 (2.6)	69.3 (1.8)	0.075
Protein (%DM)	67.6 (11.4)	64.0 (15.1)	63.4 (14.3)	64.4 (20.8)	58.9 (14.9)	0.955
Lipid (%DM)	29.7 (5.9)	47.2 (5.3)	34.9 (5.2)	23.7 (8.8)	45.4 (11.0)	0.005 ^b
Ash (%DM)	10.8 (1.9)	10.4 (2.0)	7.5 (2.1)	9.2 (1.6)	8.9 (0.6)	0.155

^a All data except moisture content presented on a dry matter basis. Values are means and one standard deviation. *N* = 3, each species

^b *P*-value significant after correction for multiple comparisons.

Table 3. Vitamin and mineral content of whole domesticated species.^a

	QUAIL	CHICKEN	RAT	MOUSE	GUINEA PIG	<i>P</i>
Retinol (IU/kg)	49 716 (27 504)	35 588 (15 309)	68 244 (23 220)	657 344 (196 887)	19 989 (3000)	<0.00001 ^b
Alpha-tocopherol (IU/kg)	60.4 (29.8)	61.4 (5.6)	210.5 (68.7)	74.4 (18.2)	29.8 (0.9)	0.00013 ^b
Calcium (mg/kg)	38 150 (7748)	24 546 (2864)	22 856 (4636)	32 076 (6185)	29 458 (4458)	0.01841
Copper (mg/kg)	2.8 (0.7)	2.7 (0.1)	1.3 (0.4)	3.8 (0.2)	6.0 (4.2)	0.04781
Iron (mg/kg)	98.7 (31.6)	97.6 (10.2)	43.0 (3.9)	76.4 (0.4)	51.9 (6.8)	0.00675
Magnesium (mg/kg)	665.6 (229.5)	535.9 (71.3)	247.3 (134.9)	431.9 (54.2)	637.3 (39.6)	0.02099
Manganese (mg/kg)	7.5 (3.2)	11.0 (1.2)	2.9 (0.9)	5.3 (1.7)	6.6 (0.5)	0.00688
Zinc (mg/kg)	54.7 (17.8)	74.1 (21.1)	35.0 (10.0)	44.0 (5.7)	64.4 (23.7)	0.09748

^a All data except moisture content presented on a dry matter basis. Values are means and one standard deviation. *N* = 3, each species

^b *P*-values significant after correction for multiple comparisons.

values for these species, which range between 55–68% for water content, 43–66% (DM) for protein content and 7–10% (DM) for ash content (Medway 1958, Lepore and Marks 1971, Brisbin and Tally 1973, Bird and Ho 1976, Thonney et al. 1984, Lavigne et al. 1994a). Lipid content appears to be the most variable component of proximate composition ranging between 19–49% (Lepore and Marks 1971, Brisbin and Tally 1973, Bird and Ho 1976, Perrigo and Bronson 1983, Thonney et al. 1984, Lavigne et al. 1994a), but there is no consistent

pattern of lipid content with respect to species, as might be expected with a labile body component.

Vitamin and mineral content in this study were much more variable than proximate composition. Although few comparative data are available, species differences in vitamin A and vitamin E content have also been found by Douglas et al. (1994), and species differences in mineral content appear to be present in the results of Bird and Ho (1976) and Lavigne et al. (1994a), although no statistical analysis of these data was presented. The pattern of

Table 4. Composition of commercial diets and relation between diet and body composition^a.

	TURKEY STARTER	MEAT- BUILDER	FORMULAB CHOW	GUINEA PIG CHOW	<i>P</i> ^b
Moisture (%)	9.3	7.7	8.9	9.4	0.900
Lipid (%)	1.1	4.2	2.0	2.4	0.192
Protein (%)	20.4	18.3	15.2	16.1	0.274
Ash (%)	7.0	5.8	7.6	8.4	0.270
Vitamin A (IU/kg)	3500	4500	6133	29 733	0.282
Vitamin E (IU/kg)	11.8	4.2	14.8	15.9	0.730
Calcium (mg/kg)	17 079	12 584	13 762	15 124	0.085
Copper (mg/kg)	18.7	14.5	13.4	14.1	0.872
Magnesium (mg/kg)	1285.1	1218.5	1068.0	1757.4	0.202
Iron (mg/kg)	161.9	154.6	239.6	290.4	0.855
Manganese (mg/kg)	76.4	78.2	16.3	54.7	0.520
Zinc (mg/kg)	127.3	124.4	99.8	90.4	0.058

^a All data except moisture content presented on a dry matter basis. *N* = 1, all diets.

^b Unadjusted *P*-values for regression of diet composition on body composition.

species differences in these studies, however, is not consistent with the pattern that we observed. For example, we observed rats to be generally low in mineral content, while Bird and Ho (1976) did not. Also, our values for vitamin E were up to 50% greater, and our values for vitamin A were up to two times greater than those of Douglas et al. (1994). Variation in nutritional content can result from differences in diet (Thonney and Ross 1987, Dierenfeld et al. 1989, Clum et al. 1996), genetics (Lepore and Marks 1971), age (Brisbin and Tally 1973, Bird and Ho 1976, Thonney and Ross 1987, Douglas et al. 1994) or sex, all of which have been demonstrated to cause significant changes in proximate composition and/or vitamin and mineral content. Diet formulation in particular has almost certainly changed over the two decades that these studies encompass, and may, therefore, be a significant source of variation. Manner and length of storage can also affect nutrient levels, particularly of vitamins, which are more labile than minerals or proximate composition. Storage may have caused the observed differences in vitamin levels between our study and that of Douglas et al. (1994), as their animals were purchased frozen from breeders whereas ours were freshly killed.

Our study suggests that species differences in nutritional content are not readily predictable. Comparative work on digestive efficiency of birds of prey has shown that the Common Buzzard (*Buteo buteo*), a generalist species, has high efficiency on a wider variety of prey than the Peregrine Falcon (*Falco peregrinus*), a specialist species (Barton and Houston 1993). Such variation in the ability to extract nutrients may partially explain the food preferences of birds in captivity. However, the prey that has the closest physical resemblance to wild prey does not necessarily bear the closest nutritional resemblance for the reasons mentioned above. If different species require prey with different nutritional content as Barton and Houston (1993) have suggested, then it is necessary to provide prey that are not only taxonomically acceptable, but nutritionally compatible for optimal breeding.

Generally, when authors allude to food quality or nutritional content they are referring to proximate composition. Although lipid content of prey may be of critical energetic importance in wild birds (Blem 1990) and does have the ability to limit egg number (Drobney 1980), lipid reserves are unlikely to be a limiting factor in the energetics or reproduction of captive birds that experience both

lower energy demands and more regular access to food. A greater potential problem in captivity is egg and chick viability, which is not limited by lipid and protein reserves, but can be severely affected by vitamin and mineral content of food (NRC 1984, Naber and Squires 1993).

All prey analyzed in this study met known requirements of domestic mammalian carnivores for vitamin A, Ca, Mg and Zn (vitamin A, 2440–10 000 IU/kg; Ca, 0.4–1.2%; Mg, 0.04–0.1%; Zn, 30–50 mg/kg; NRC 1985, 1986, Robbins 1983). Copper levels were inadequate in all species except guinea pigs, Fe was below recommended levels in rats and guinea pigs and Mn was lower than suggested in rats (Cu, 5.0–7.3 mg/kg; Fe, 60–100 mg/kg; Mn, 5–10 mg/kg; NRC 1982, 1985, 1986). Manganese deficiency has recently been documented in captive raptor chicks fed exclusively rats (C. Sandfort, pers. comm.). Although all species except guinea pigs met recommended levels of vitamin E for mammalian carnivores (20–80 IU/kg, NRC 1982, 1985, 1986), it has been suggested that raptors may require up to 10 times more vitamin E to protect against deficiencies (Calle et al. 1989, Dierenfeld et al. 1989). Other differences between nutrient requirements for domestic mammalian carnivores and nondomestic avian carnivores may exist.

ACKNOWLEDGMENTS

We would like to thank A. Sirles and G. Thomas for care and maintenance of research animals. We also thank J. Rigg, B. Bammel and J. Munger for advice and access to additional laboratory space and equipment and L. Pearson and D. Barker for their laboratory assistance. This research was made possible by donations of equipment from Perkin-Elmer, Corning, Milton Roy, Precision Scientific and Nalge. This manuscript benefited from helpful comments by D. Bird, T. Cade, G. Duke, J. Gesaman, J. Linthicum and C. Marti.

LITERATURE CITED

- BARTON, N.W.H. AND D.C. HOUSTON. 1993. A comparison of digestive efficiency in birds of prey. *Ibis* 135: 363–371.
- BEDI, K.S. 1987. Lasting neuroanatomical changes following undernutrition in early life. Pages 1–49 in J. Dobbing [ED.], *Early nutrition and later achievement*. Academic Press, London, U.K.
- BLEM, C.R. 1990. Avian energy storage. Pages 59–113 in D. Power [ED.], *Current Ornithology*, Vol. 7. Plenum Press, New York, NY U.S.A.
- BIRD, D.M. AND S.K. HO. 1976. Nutritive values of whole-animal diets for captive birds of prey. *Raptor Res.* 10: 45–49.
- BRISBIN, I.L., JR. AND L.J. TALLY. 1973. Age-specific

- changes in the major body components and caloric value of growing Japanese quail. *Auk* 90:624–635.
- CALLE, P.P., E.S. DIERENFELD AND M.E. ROBERTS. 1989. Serum alpha-tocopherol in raptors fed vitamin E-supplemented diets. *J. Zoo Wildl. Med.* 20:62–67.
- CLUM, N.J., M.P. FITZPATRICK AND E.S. DIERENFELD. 1996. Effects of diet on nutritional content of whole prey. *Zoo Biol.* 15:525–537.
- COMBS, S.D. AND G.F. COMBS, JR. 1985. Varietal differences in the vitamin E content of corn. *J. Agric. Food Chem.* 36:815–817.
- DIERENFELD, E.S. 1994. Vitamin E in exotics: effects, evaluation and ecology. *J. Nutr.* 124:2579S–2581S.
- , C.E. SANDFORT AND W.C. SATTERFIELD. 1989. Influence of diet on plasma vitamin E in captive Peregrine Falcons. *J. Wildl. Manage.* 53:160–164.
- , N.J. CLUM, E.V. VALDES AND S.E. OYARZUN. 1994. Nutrient composition of whole vertebrate prey: a research update. Proc. Assoc. Zoo Aquaria Conf., Atlanta, GA U.S.A.
- DOUGLAS, T.C., M. PENNINO AND E.S. DIERENFELD. 1994. Vitamins E and A, and proximate composition of whole mice and rats used as feed. *Comp. Biochem. Physiol.* 107A:419–424.
- DROBNEY, R.D. 1980. Reproductive bioenergetics of wood ducks. *Auk* 97:480–490.
- ELLIS, R.L. 1984. Meat and meat products. Pages 431–443 in S. Williams [Ed.], Official methods of analysis. Association of Official Analytical Chemists, Inc., Arlington, VA U.S.A.
- GERSHWIN, M.E., R.S. BEACH AND L.S. HURLEY. 1985. Nutrition and immunity. Academic Press, San Diego, CA U.S.A.
- GOOD, R.A. AND A.J. GAJJAR. 1986. Diet, immunity and longevity. Pages 235–250 in M.L. Hutchinson and H.N. Munro [Eds.], Nutrition and aging. Academic Press, San Diego, CA U.S.A.
- GRANTHAM-MCGREGOR, S. 1987. Field studies in early nutrition and later achievement. Pages 128–174 in J. Dobbing [Ed.], Early nutrition and later achievement. Academic Press, London, U.K.
- HORWITZ, W. [Ed.] 1975. Official methods of analysis of the Association of Official Analytical Chemists. Assoc. Off. Analyt. Chem., Washington, DC U.S.A.
- LAVIGNE, A.J., D.M. BIRD, D. LACOMBE AND J.J. NEGRO. 1994a. Growth of hand-reared American Kestrels I. The effect of two different diets and feeding frequency. *Growth Dev. Aging* 58:191–201.
- . 1994b. Growth of hand-reared American Kestrels II. Body composition and wingloading of fledglings hand-fed two different diets. *Growth Dev. Aging* 58:203–209.
- LEPORE, P.D. AND H.L. MARKS. 1971. Growth rate inheritance in Japanese quail. 4. Body composition following four generations of selection under different nutritional environments. *Poult. Sci.* 50:1191–1193.
- MACHLIN, L.J. 1984. Vitamin E. Pages 99–146 in L.J. Machlin [Ed.], Handbook of vitamins: Nutritional, biochemical and clinical aspects. Marcel Dekker, Inc., New York, NY U.S.A.
- MEDWAY, W. 1958. Total body water in growing domestic fowl by antipyrine dilution technic. *Proc. Soc. Exp. Biol. Med.* 99:733–735.
- NABER, E.C. AND M.W. SQUIRES. 1993. Vitamin profiles of eggs as indicators of nutritional status in the laying hen: diet to egg transfer and commercial flock survey. *Poult. Sci.* 72:1046–1053.
- NATIONAL RESEARCH COUNCIL. 1982. Nutrient requirements of minks and foxes. National Academy Press, Washington, DC U.S.A.
- . 1984. Nutrient requirements of poultry. National Academy Press, Washington, DC U.S.A.
- . 1985. Nutrient requirements of dogs. National Academy Press, Washington, DC U.S.A.
- . 1986. Nutrient requirements of cats. National Academy Press, Washington, DC U.S.A.
- OLSON, J.A. 1984. Vitamin A. Pages 1–44 in L.J. Machlin [Ed.], Handbook of vitamins: nutritional, biochemical and clinical aspects. Marcel Dekker, Inc., New York, NY U.S.A.
- PALMER, R.S. 1988. Handbook of North American birds. Vols. 4 and 5. Yale Univ. Press, New Haven, CT U.S.A.
- PARKER, H.E. 1963. Magnesium, calcium and zinc in animal nutrition. *Atomic Absorption Newsletter* 2:23.
- PERRIGO, G. AND F.H. BRONSON. 1983. Foraging effort, food intake, fat deposition and puberty in female mice. *Biol. Reprod.* 29:455–463.
- RICE, W.R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- ROBBINS, C.T. 1983. Wildlife feeding and nutrition. Academic Press, Orlando, FL U.S.A.
- SKLAN, D., D. MELAMED AND A. FRIEDMAN. 1995. The effect of varying dietary concentrations of vitamin A on immune response in the turkey. *Br. Poult. Sci.* 36:385–392.
- TAYLOR, S.L., M.P. LAMBEN AND A.L. TAPPEL. 1976. Sensitive fluorometric method for tissue tocopherol analysis. *Lipids* 11:530–538.
- THONNEY, M.L. AND D.A. ROSS. 1987. Composition of gain of rats fed low or high protein diets and grown at controlled rates from 80 to 205 grams. *J. Nutr.* 117:2135–2141.
- , A.M. OBERBAUER, D.J. DUHAIME, T.C. JENKINS AND N.L. FIRTH. 1984. Empty body component gain of rats grown at different rates to a range of final weights. *J. Nutr.* 114:1777–1786.
- WILKINSON, L. 1990. SYSTAT: The system for statistics. Systat, Inc., Evanston, IL U.S.A.

Received 3 August 1996; accepted 22 April 1997